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Review

Global positioning system and associated technologies in animal behaviour and ecological research

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Biologists can equip animals with global positioning system (GPS) technology to obtain accurate (less than or equal to 30 m) locations that can be combined with sensor data to study animal behaviour and ecology. We provide the background of GPS techniques that have been used to gather data for wildlife studies. We review how GPS has been integrated into functional systems with data storage, data transfer, power supplies, packaging and sensor technologies to collect temperature, activity, proximity and mortality data from terrestrial species and birds. GPS ‘rapid fixing’ technologies combined with sensors provide location, dive frequency and duration profiles, and underwater acoustic information for the study of marine species. We examine how these rapid fixing technologies may be applied to terrestrial and avian applications. We discuss positional data quality and the capability for high-frequency sampling associated with GPS locations. We present alternatives for storing and retrieving data by using dataloggers (biologging), radio-frequency download systems (e.g. very high frequency, spread spectrum), integration of GPS with other satellite systems (e.g. Argos, Globalstar) and potential new data recovery technologies (e.g. network nodes). GPS is one component among many rapidly evolving technologies. Therefore, we recommend that users and suppliers interact to ensure the availability of appropriate equipment to meet animal research objectives.

Keywords: global positioning system technology; radio-tracking; biotelemetry; animal behaviour; animal ecology; datalogging

1. GPS: HISTORY

During the past 35 years, new technologies have been developed for remotely tracking and studying free-ranging animals (Fuller *et al.* 2005), and advances in technology continue to increase opportunities for incorporating tracking and biotelemetry to study animal behaviour and ecology (Cooke *et al.* 2004; Ropert-Coudert & Wilson 2005; Hooker *et al.* 2007; Ponganis 2007; Rutz & Hays 2009). Perhaps the most revolutionary advance in obtaining animal locations is the use of GPS (see definitions in glossary at end of this paper; see also Sibbald & Gordon 2001). It is useful to know some of the history and the capabilities of GPS because the types of data obtained since the early use of GPS have changed with the ongoing rapid advances that have occurred in technology. We review history that is informative for understanding results and interpretations based on previous GPS equipment, and we describe the current GPS and associated technology to provide a basis for biologists who are considering telemetry to address their objectives, and for use with contemporary analytical methods and modelling efforts (Cagnacci *et al.* 2010; Hebblewhite & Haydon 2010).

There are advantages to obtaining animal positions from GPS over other technologies (Rodgers *et al.* 1996). GPS allows position determination on the surface of the Earth and in the air. GPS systems are highly accurate and repeatable compared with ground-based conventional very high frequency (VHF) triangulation techniques (Coelho *et al.* 2007) and VHF tracking from aircraft or Argos satellite Doppler-based positioning (Soutullo *et al.* 2007). GPS has 24-hour coverage, with position updates available in rapid succession (one location update per second is typical). Such data can be reviewed, selected, filtered and/or statistically analysed to help ensure accuracy

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(Frair *et al.* 2010). GPS often allows positions in bad weather when other approaches can be restricted. Finally, the GPS system provides accurate time stamping of a position. When GPS was coupled with data transmission technologies (Rempel *et al.* 1995; Rodgers *et al.* 1996; Schwartz & Arthur 1999), a new era of animal tracking began, and recent literature contains numerous examples of successful studies using GPS positioning (Godley *et al.* 2008; Gremillet *et al.* 2008; Laurian *et al.* 2008; Trathan *et al.* 2008; Van Beest *et al.* 2010).

(a) *GPS: a brief system overview*

The GPS, also known as NAVSTAR, began in 1973 when the United States Department of Defense developed a satellite-based three-dimensional positioning system with 24-hour worldwide coverage. The initial design was four satellites to be in view from any position on the Earth's surface at any time. The concept was based on a receiver's distance from a satellite being estimated by measuring the time for the signal to travel from the satellite to a GPS receiver. Measuring the time from each of the four satellites (of known positions) allows three-dimensional position fixing (latitude, longitude and altitude) to be determined at the GPS receiver.

As initially conceived, the GPS system comprises three functional segments:

— The space segment is 24 satellites, each orbiting about 20 200 km above the Earth, approximately every 12 h. The design uses two downlink frequencies: L1 and L2. L1 is for non-military users and carries the CA (Coarse/Acquisition) and P (Precise) codes; L2 carries only the P code. The military is able to reduce ionospheric errors by using a two-frequency (L1 and L2) approach in their receivers.

— The operational ground control segment includes five tracking stations distributed throughout the world. The master control station is at the Consolidated Space Operational Center in Colorado Springs, CO, USA.

— The user segment is a GPS receiver designed to track, measure time of signal arrival, demodulate and use navigation messages.

At first, the military retained the most precise system operation exclusively for its own use, and intentionally degraded the performance accuracy for non-military applications. This approach, called selective availability (SA), was initiated in March 1990. SA degraded the performance of non-military applications to approximately 100 m. Interestingly, differential GPS (DGPS) has been developed by commercial users as an independent means of reducing the SA error (Moen *et al.* 1997; Rempel & Rodgers 1997). The position error introduced by SA was minimized by establishing observed errors of a receiver at a known location, and applying the observed errors as a correction factor to other GPS receivers to obtain their 'true' position. By using DGPS, most induced errors can be removed (Hogarth 1991; Sandlin *et al.* 1995; Parkinson 1996; Spilker & Parkinson 1996). SA was suspended in May 2000 and permanently decommissioned in September 2007 (Kovach & Van Dyke 1998). Commercial users have since enjoyed typical horizontal position errors of less than 30 m (D'Eon *et al.* 2002; Frair *et al.* 2010). Commercial users will soon benefit from the addition of a second frequency (L4), to reduce ionosphere-induced errors and increase typical accuracy performance to 6 m (Sandlin *et al.* 1995). We have been unable to find any wildlife study reporting that GPS outages in the space and/or ground station segments has resulted in a significant loss of positional data, leading us to conclude that GPS as a system has been extremely reliable and has provided virtually uninterrupted service since wildlife studies began using the system in the mid-1990s.

2. TRANSFORMING GPS INTO AN ANIMAL TRACKING SYSTEM

Fully functional GPS tracking systems for wildlife developed as commercial GPS technology matured and was integrated with other diverse technologies. Early receivers required 10–30 min to find GPS satellites and determine their first position. Many early receivers required a complete download of an almanac on first power up, which took 13 min. In addition, when the GPS satellite constellation was incomplete it was sometimes necessary for the receiver to wait for a sufficient number of satellites to come into view. Even with the almanac cold starts could take 5 min (table 1). To speed up the process, receivers were provided with GPS time and a general location to create a warm start, and the newest receivers now use thousands of correlators, resulting in even faster satellite acquisition. Minimizing time to first fix (TTFF; 'fix' = location estimate) was critical for animal tracking because the receiver is usually turned on and off over time to minimize current consumption and extend system life. Also, the satellite constellation, now complete with backup satellites, is more constant and predictable, and GPS receiver sensitivity has increased. Today, TTFF after start-up is typically 30 s or less with a good antenna and clear view of the sky (table 1).

The first GPS receivers were developed by Magellan in 1989 and weighed 840 g with a volume of 885 cm^3. These were therefore impractical for animal applications. Large commercial markets have been responsible for the rapid advances in GPS receiver technology. By the mid-1990s, the larger GPS manufacturing companies shifted their marketing plans to the manufacturing of receiver engines and chip sets. These engines were procured by second-tier companies and integrated into specific original equipment manufacturing (OEM) applications, such as wildlife tracking. Fuelled by the requirement in the United States to be able to locate all mobile phones in emergencies, GPS engines became smaller and more energy-efficient, and therefore more usable for animal-tracking applications. Smaller, low-voltage (3.0 Vdc) and low-current (less than 30 mA) receivers are better integrated with battery-powered systems that now allow tracking of smaller mammalian species and, more recently, birds (Ryan *et al.* 2004; Meyburg

Table 1. Typical specifications of representative GPS receiver modules considered appropriate for incorporation in animal-borne systems. Sources: SVeeSIX-CM-2 6-channel miniature GPS module: 1-850 0213-2/94, Trimble Navigation Ltd., Sunnyvale, CA. Lassen SK8 Sierra series GPS receiver: TID10506 (3/96), Trimble Navigation Ltd., Sunnyvale, CA. Lassen LP GPS low-power module for portable applications: TID 11547D (08/03), Trimble Navigation Ltd., Sunnyvale, CA. NEO-5 u-blox ROM-based GPS modules: GPS-G5-MS5-07025-3, u-blox AG, Thalwil, Switzerland.

model number	channels	year	length × width (mm)	operating voltage/current (V/mA)	acquisition time cold/warm/hot (s)
SVeeSIX-CM-2	6	1994	82.6 × 46.5	5/250	120–300/50/30
Lassen SK8	8	1996	82.6 × 31.2	5/150	<120/45/<20
Lassen LP	2	1999	66.2 × 31.8	3.3/55	<130/<42/<15
NEO-5	50	2009	16.0 × 12.2	3.0/43	29/29/<1

et al. 2006, 2007; Gremillet *et al.* 2008; Mandel *et al.* 2008), which for some species requires special attachments (e.g. Tyler & Flint 2008). Even with the new low-power GPS receiver technology and using solar power to recharge energy storage devices, receiver power management is critical in finding a threshold between device weight and operational life.

The success of animal-borne GPS systems is at least in part due to lessons learned from experience with earlier tracking technologies, including conventional VHF and Argos systems. Many wildlife species live in extreme environments and expose instruments to levels of shock and extreme temperatures beyond the range of conditions typically experienced by electronics carried by humans. Applying GPS to wildlife tracking applications requires many innovations. Marine species spend their lives in saltwater that blocks VHF and UHF transmissions and GPS downlink signals, only exposing a receiver or transmitting antenna for a short time when the antenna is above the surface. The requirement for unattended long operational life of 6 months to several years is critical to wildlife applications and seldom a commercial requirement. Telemetry designers/manufacturers must select the appropriate technologies available in the commercial and military world, and integrate those into specialized instruments with rigorous performance requirements specific to wildlife. This process requires professionals who understand both the electronics and the wildlife labouring in concert to be successful.

A significant limitation of the basic GPS system was the lack of a means to relay information from the instrumented animal to another location. It was clear that data transfer technologies would be required to transform GPS into a tracking system for oceanographic buoys, meteorological balloons and animals. The data relay segment of practical animal tracking systems (see §4) has developed independently of the GPS system.

3. FILLING THE GAPS BETWEEN FIXES

Currently, GPS location can be updated by the second. Unfortunately, updating at this rate exceeds the available power restrictions for most animal systems. As advances occur in battery technology, such as decreased GPS power requirements and increased onboard memory capacity, biologists will be able to track diverse species and know where an animal is at all times. In the interim, there has been progress embedding inertial navigation devices into GPS devices to allow the estimation of animal locations on a continuous basis between GPS fixes (Hunter *et al.* 2005; Elkaim *et al.* 2006). An inertial navigation device can be developed using a pedometer, electronic compass and three-dimensional accelerometer (Mitani *et al.* 2003). Resulting data can be used to plot the location of an animal in continuous time. Inertial navigation systems suffer from deteriorating accuracy as errors compound over time, but GPS fixes at sufficient intervals can be used to reset the accuracy of the estimated track (Hunter 2007; Wilson *et al.* 2007).

(a) *Rapid fix technologies reduce TTFF*

Navigation data including ephemeris data and GPS receiver observations (especially pseudoranges) are needed to obtain accurate GPS location estimates; however, acquiring the ephemeris data contained in the navigation message from individual satellites is responsible for a large portion of the time delay in obtaining a first fix from warm or cold start conditions. The delay limits the usefulness of standard GPS when a rapid 'time to fix' is essential, as is the case of marine mammals. The receiver can be kept in a 'hot' start mode and thus often acquire a GPS fix of a surfacing animal in 10 s (Elkaim *et al.* 2006). Unfortunately, current consumption in this mode is high. Alternatively, the GPS receiver can calculate the pseudoranges and shut down before recovering the ephemeris data, which are obtained later from a website, and then the location is calculated in post-processing. Two additional rapid fixing technologies have recently emerged (figure 1).

(i) *Quick fix pseudoranging*

Systems with quick fix pseudoranging (QFP) were designed for marine mammal and sea turtle applications.

QFP systems can use standard GPS receivers and, within 5 s of surfacing, can determine the pseudorange and obtain the information necessary for post-processing locations at a later time. Preliminary QFP accuracy testing suggests that error is typically less than 75 m (S. M. Tomkiewicz 2010, personal communication). All data necessary for post-processing can be obtained from four to eight GPS satellites.

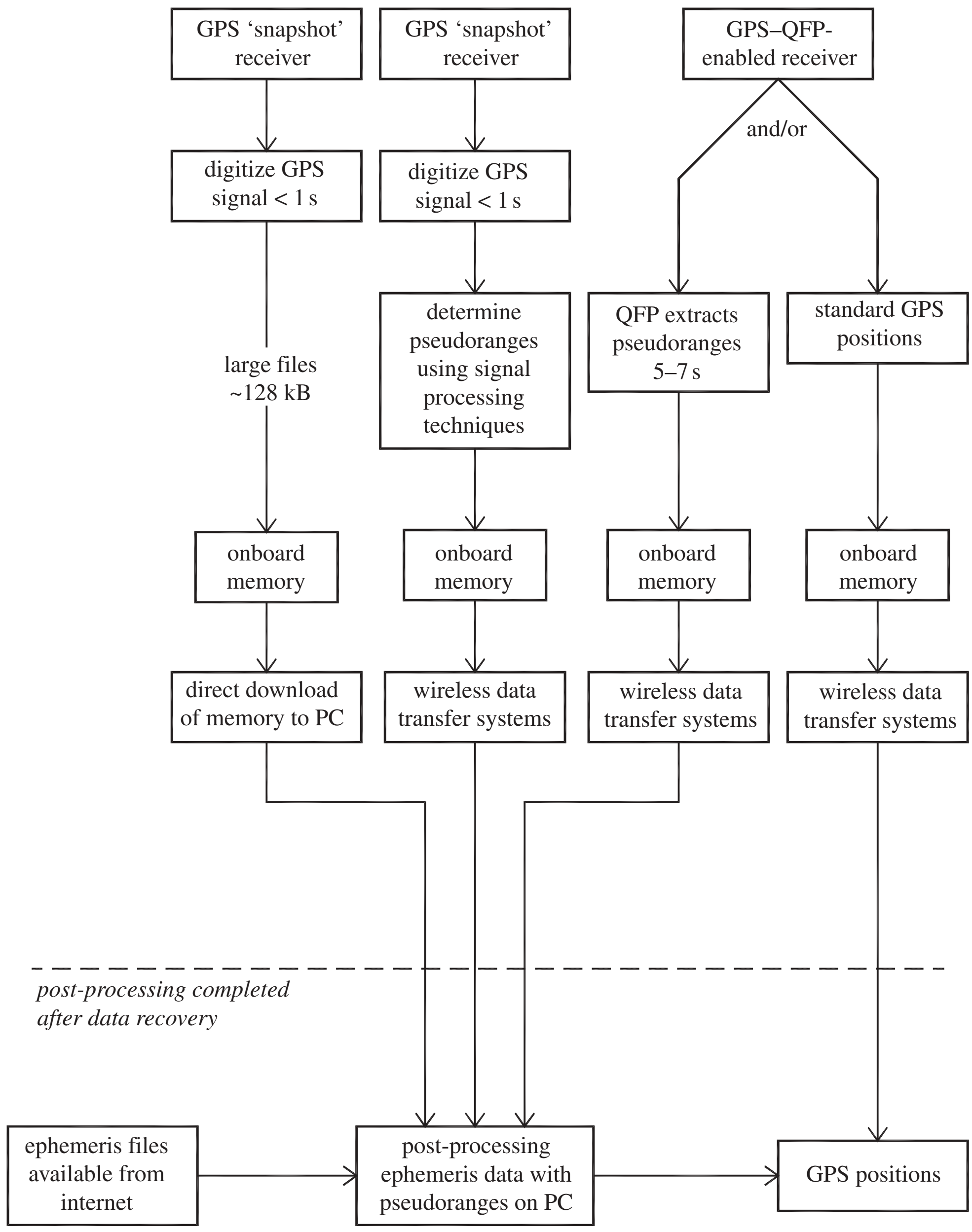

Figure 1. Flow diagram of three 'rapid fix' technologies currently used in animal applications. All three rapid fix technologies require post-processing to obtain the GPS-based locations, usually after the files are recovered by the researcher. Snapshot receivers can obtain their data in sub-second exposure times but the resulting large files must be further processed to be small enough to be transferred via wireless technologies currently in use. QFP can provide rapid fix (in 5–7 s), or when conditions allow, a standard GPS fix (in 20–30 s).

These data can be compressed into a single Argos satellite system (see below) uplink message with an error detection byte, transmitted and recovered via the Argos data collection and location satellites (DCLS) system or other data recovery technology. As a backup to the transmitted data via Argos, all pseudorange data and time stamps are stored onboard the unit for direct download if the unit is recovered.

When recovered via Argos, the data are processed to obtain a QFP position automatically with specialized software such as the Telonics Data Converter (TDC; Teleonics 2009). TDC runs on a standard PC and can accept data from the Argos data dissemination system, obtain all required ephemeris data, process and sort dive information, standard GPS positions and QFP positions, and provide a spreadsheet compatible report (Teleonics 2009).

It is important to note that a QFP unit is adaptive and can obtain standard high-accuracy GPS-based locations when adequate surfacing time occurs. The unit can store all standard GPS-based locations and compress up to 10 historical GPS-based locations in a single Argos message, thus providing very efficient data transfer. Also, the unit can precisely calculate Argos satellite overpasses and transmit only when satellites are visible to the unit. When animal surface times are brief (e.g. less than 5 s), the functions of systems that integrate QFP and GPS combine for efficient use of the onboard battery, and a high probability of location accuracy and data transfer using Argos DCLS.

(ii) *Snapshot receivers*

Snapshot receivers are not conventional GPS receivers. These specialized receivers are designed to digitize GPS downlink signals in less then a second. Once a snapshot (digitized data) is obtained, there are two ways to proceed. (i) The digitized data can be stored in 'raw form'. This approach has the advantage of very low power consumption, but the disadvantage is that the datasets required for a small number of GPS-based locations fixes create files so large that data transfer using the existing data transfer technologies (see below) becomes impractical. The current use of this methodology is to store digitized data in large non-volatile memory until the unit can be recovered. (ii) The second approach involves extracting and calculating the pseudorange from the digitized signal. This approach entails extensive signal processing onboard the animal-borne unit, which requires substantial power and onboard processing time, but results in a dataset that is smaller and can be treated in the same way as the QFP pseudorange data described above. These datasets can be transferred using the existing data transfer technologies. Both implementations estimate a location using post-processing by collecting appropriate data in a few hundred milliseconds. Studies are under way in the Amazon rainforest (MacLean 2009) and on penguins (Trathan *et al.* 2008) using the first approach, while the second has been applied to studies on marine mammals and sea turtles that require remote data recovery (Hazel 2009). This second approach has been called 'Fastloc GPS' and has typically been used for data recovery using Argos (Kuhn *et al.* 2009). A disadvantage of both techniques is that the unit cannot determine its own position. Not knowing the current position has implications for the efficiency of 'Fastloc' data transfer via Argos (see §3*a*(i)).

4. INTEGRATING GPS AND DATA RETRIEVAL SYSTEMS

Animal-borne GPS systems are not simple hand-held GPS receivers that are strapped on to the animal. The manufacturers of biotelemetry devices integrate the GPS receiver as they would any other sensor into a complete system for deployment on wildlife. The workhorse of all wildlife GPS systems is the micro-power data acquisition/controller (MDAC; figure 2). The MDAC manages the entire application to achieve a functional system by controlling numerous individual tasks, including:

— Turning on and off the GPS receiver, sensors and data transfer components to manage the energy budget and acquire positions at sampling times appropriate for the research goals. Often samples are taken under complex scheduling regimes (sometimes termed duty cycles) that can be programmed to change over the course of the year or study.
— Interfacing via signal processing with onboard sensors, collecting and storing data to memory (e.g. activity, temperature, dive data).
— Providing an interface so the user can program parameters and download stored data.
— Controlling a VHF beacon that transmits a pulse rate (not GPS-based location data), which indicates that the GPS unit is operating correctly.
— Controlling a VHF beacon to report mortality events.
— Controlling the seasonal duty cycling of the VHF beacon and the means to relocate the collar for recovery and refurbishment.
— Managing the VHF beacon to avoid interference with GPS signals.
— Managing the wireless data transfer in those units equipped with that technology.

System and information management by the MDAC allow for the gathering, organization and storage of data. The next step is conveying the data to the user. Many data retrieval systems have been developed to meet various study circumstances, including reducing the potential disturbance to radio-marked animals.

(a) *Store onboard systems*

In some applications, GPS data can be acquired and stored in the unit and then downloaded from the memory when the unit is recovered. These systems can store GPS-based locations, pseudoranges or digitized GPS signals along with other sensor data (e.g. activity, dive information, temperature) and are often called store onboard (SOB) systems. Historically, systems developed for terrestrial animals stored GPS-based locations and over time added sensor data (e.g. activity), whereas systems developed for marine applications (typically called biologgers) stored sensor data (e.g. dive information) and have over time integrated GPS-based locations. Both disciplines have benefited from obtaining both sensor and positional data to provide a deeper understanding of the biology of the animal. SOB units can be in the field several years before any data are recovered (Rice 2008). SOB is less expensive than incorporating a wireless data transfer system, but there is the risk that the unit is not recovered and the data are lost. The development of accessory devices, such as programmable release mechanisms and the integration of VHF-tracking beacons, has increased the likelihood of recovering SOB units (Merrill & Mech 2003; Sager-Fradkin *et al.* 2008; Claridge *et al.* 2009). Studies employing the SOB approach are commonplace (Barbari *et al.* 2006; Sawyer *et al.* 2006; Kumpula & Colpaert 2007; Guilford *et al.* 2008; Rice 2008).

In the mid-1990s, the first SOB units stored only about 1000 positions in their limited memory. Now, inexpensive, highly dense non-volatile memory in micro-miniature packages allows saving greater amounts of GPS and sensor data. User-friendly programming software allows independent duty-cycling of sensors and complex sensor-sampling schedules. The large capacity of datalog memory enables some sensor sampling rates near 1 Hz.

Generally, current GPS–SOB systems can store about 12 000 GPS-based locations in 0.33 MB of memory powered by a single D-cell-sized primary

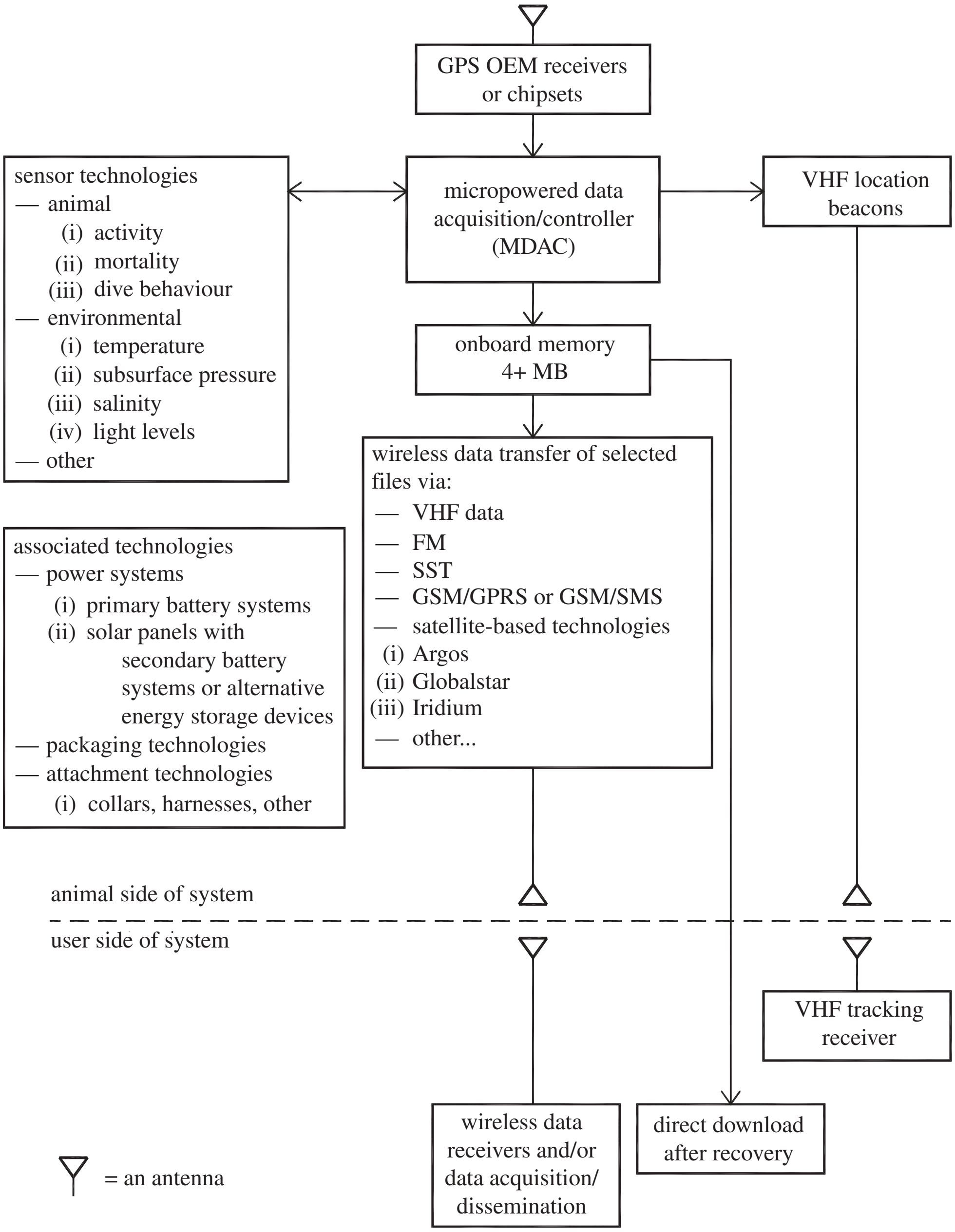

Figure 2. Block diagram showing the components of a GPS positioning and data collection system suitable for deployment on animals. Note that many of these components were designed specifically for these applications.

lithium battery. It is not uncommon for GPS subsystems to have 8–16 MB of memory, and much more could be added. In fact, most GPS systems are not memory-limited at all; the operational life is limited by the battery capacity, which is largely used to collect GPS position data, sensor data and housekeeping functions. Very little energy is used to download data as this occurs only after the unit is recovered, making SOB most efficient for maximizing GPS location and sensor data collection.

(b) *GPS subsystems with remote data transfer capabilities*

Many study designs require that GPS-based locations and other data be recovered during the deployment period. In fact, several countries are developing ethical regulations to ensure that the interference with animals will result in actual data reception by researchers (H. Dettki 2010, personal communication). Remote data transfer techniques can be incorporated to send data at regular intervals or near-real-time, especially for some applications that use recent data as a basis for implementing additional fieldwork such as finding a nest, den or predation site, or for adaptive management when animals begin using a certain area. Most GPS systems with data transfer technology also retain location and sensor data as an SOB, so that data can be downloaded if the unit is recovered. This provides a backup dataset should the remote transfer become inoperable while on the animal.

(i) *Data recovery using a VHF beacon data transmitter*

A special version of the conventional VHF beacon is used to encode GPS-based location data on the VHF beacon data transmission. This data transfer method has the advantage of using a beacon, which normally is used for locating the animal, already onboard the system (Stoner *et al.* 2008; Krone *et al.* 2009). Small amounts of data can be continually transmitted during 'on periods' of the VHF beacon data with little additional current consumption. However, power source restrictions do limit the VHF beacon data transmission to a narrow bandwidth and thus a very limited data rate. Systems using this approach can take upwards of 7 s to transfer a single GPS-based location and 45 min to transfer approximately 180 positions. In one study, aircraft typically circled 600–800 m from the animal to remain within the reception range of the VHF signal (G. B. Stenhouse 2010, personal communication). Long upload sessions and the possible requirements for re-establishing communication if the link is disrupted might result in excessive disturbance and disruption of normal behaviour of the subject animal. Furthermore, with ever-increasing volumes of data from GPS systems, this approach is limiting when compared with other data transfer technologies and highly subject to noise interference. This VHF system is suited for situations in which small amounts of the GPS data are required in real time, while the remaining data can await downloading from the recovered units.

(ii) *Data recovery using radio modem technology*

Modems MODulate and DEModulate data, and can use different segments of the radio-frequency spectrum and modulation technologies. Among these technologies is single-channel narrow-band frequency modulation (FM). FM transceivers are commonly used to recover data from remote-fixed site instruments. In animal applications, single-channel FM modems are subject to problems such as interference on a selected channel. Also, unrestricted movement of instrumented animals means they must be classified as mobile systems, limiting the number of systems that can be deployed in a given area. Additionally, single-channel FM data modems require individual frequency allocation and licensing (Clark *et al.* 2006). Nevertheless, single-channel modem technology has proven useful for some wildlife applications (Rice *et al.* 2009).

A solution to minimize interference is found in spread spectrum technology (SST). SST allows data packets to be spread over many frequencies either through a technique called direct sequence coding or through frequency hopping. Using frequency hopping, the data packets are transferred on different frequencies in a pseudorandom manner. Packets transmitted on a frequency that experiences noise or interference are noted as damaged or missing and then retransmitted on another frequency that is probably free of the interference. Many SST units can successfully transfer data in an area, and even areas that contain single-channel narrow-band FM units (Kesteloot & Hutchinson 1997). SST is well suited for mobile applications like animal tracking, where chance encounters with other devices are expected (Clark *et al.* 2006). This technology also allows the user to operate unlicensed at power levels up to 1 W, which makes long-range data recovery from the ground or to aircraft possible.

Current SST systems optimize bandwidth and modulation to achieve high-speed data transmission and long-range performance (e.g. recovering 15–30 GPS-based locations per second). The download sequence is initiated by an SST transceiver connected to the researcher's laptop computer. However, the animal-borne radio modems cannot be in the receiving mode continuously; they must be duty-cycled to minimize current consumption. Typically, there are preprogrammed schedules at times when the researcher can be present to download the data. The line-of-sight range of the system is typically 1.5 km ground-to-ground and approximately 6–10 km to a transceiver in an aircraft.

The GPS–SST system uses substantially less power (typically less than 5% of the power budget is used for data transfer) than some other alternatives like Argos when large amounts of data must be transferred. The protocol effectively and automatically recovers missing data packets to form a complete dataset over the specified time frame. The SST system also has the advantage that in addition to downloading data on command, the two-way link can be used to adjust the duty cycle, sampling rates or other functionality of the GPS–SST system. Below, we present some data recovery alternatives that do not require retrieving a SOB or having personnel in the field, and that provide greater geographical coverage.

(iii) *Data recovery using Argos DCLS*

The Argos DCLS is carried onboard the National Oceanographic and Atmospheric Administration (NOAA) low-earth-orbit (LEO) satellites and the European Organization for the Exploitation of Meteorological Satellites (EUMETSAT) MetOp-A satellite, and will be carried on other LEO satellites to be launched by other countries. Argos presents many advantages as a data transfer system, including worldwide coverage and an established history of use in animal applications since the 1980s (Harris *et al.* 1990). International funding and government commitments for Argos help assure a secure future. The Argos system can provide supplemental sensor data (e.g. temperature, activity) and positions based on Doppler measurements of the Argos transmitter's uplink frequency. Although these positions are often less accurate (hundreds of metres to kilometres), they provide a backup to GPS positioning (Collecte Localisation Satellites 2008*b*). Argos is used as a data transfer system for animal-borne GPS (Yasuda & Nobuaki 2005; Meyburg *et al.* 2007; Cain *et al.* 2008; Mandel *et al.* 2008).

Argos satellites orbit about 850 km above the Earth (Collecte Localisation Satellites 2008*b*), thereby allowing the use of low-power transmitters (100 mW to 1 W) with small omnidirectional antennas. Current Argos systems specification (uplink centre frequency at 401.650, data rate of 400 bits s^{-1}, uplink message length 31/32 bytes, two to five satellites in constellation) and sophisticated data compression in the animal-borne units enable transferring about 24–48 GPS-based locations per day from collar-mounted units on medium- to large-sized animals, and up to 6–10 GPS-based locations from smaller avian units. Data can be recovered as frequently as daily; however, intensive use of the transmitter is a significant drain from the limited energy budget of an animal-borne unit, and thus limits the number of GPS-based locations that can be acquired. A well-planned data recovery schedule must be established to balance data collection and data recovery operational life.

The GPS reception and Argos transmission schedule is especially important when radio-marking birds, for which the mass of the unit is usually restricted to 3 to 5 per cent of the bird's body mass. Recent developments allow the GPS data in the animal-borne Argos–GPS unit to be used with onboard orbital prediction programs enabling transmissions only during satellite overpasses. This increases data transfer and power efficiency for the system. When GPS transfer via Argos is applied to birds, solar charging often is used to prolong unit operation life (Soutullo *et al.* 2007).

Many factors can affect the regularity and extent of solar charging (e.g. hours of light, cloud cover), and thus the performance of the unit. We suggest that biologists test unit performance. For example, as a simple first test, we placed four GPS–Argos patagial wing tags with the solar array parallel to a flat roof, approximately 4 m above ground level, exposed to clear, unobstructed sky. From 22 possible GPS location estimate opportunities, we obtained fixes approximately 69 per cent of the time (range 55–95%). The horizontal location error averaged 15 m (range 10–518 m), while the 75th percentile for the four units was 17 m. The average altitude error was 77 m above the test site elevation, which was well within the 220 m nominal accuracy for the high-altitude calibration offered by the manufacturer.

For animal tracking, Argos is a one-way random access system, and some manufacturers preprogram wildlife units to transmit in certain time slots when numerous satellite overpasses are predicted as a means to conserve energy. A two-way Argos link is being tested on the Metops A satellite. Presently, the receiver is too large and consumes too much power to be practical for animal tracking. However, technology advances might make some two-way applications possible for future wildlife studies (Vassal 2006), thus enabling further energy budget efficiencies.

A geographical limitation with Argos is that noise in the environment in Europe and Mongolia–Pakistan disrupts data transfer on the Argos uplink frequency (Collecte Localisation Satellites 2006; Hughes 2008). To mitigate this, authorities are using international agreements to protect satellite uplink frequencies (Collecte Localisation Satellites 2006, 2008*a*) and technological solutions that include using high-power Argos transmitters or more exposed or modified antenna designs to achieve higher radiated power for a functional satellite link. Increased power will affect operation schedules and lifetime, and modified antenna designs increase antenna exposure and are subject to fatigue and breakage on the animal.

(iv) *Data recovery using global system for mobile communications*

Some GPS systems deployed on animals use GSM telephone data services (Gervasi *et al.* 2006; Godvik *et al.* 2009; Kojola *et al.* 2009). Two GSM technologies are used in animal-borne systems. GSM/SMS (global system for mobile communications/short message service) services allow the transfer and regular updating of GPS-based locations (six to eight positions per GSM per SMS message) and some limited data (e.g. mortality events). Text message lengths are short (up to 1120 bits and data rates of 9.6 kbps). Larger datasets (e.g. activity data) use General Packet Radio System (GSM/GPRS) services when available (R. Schulte 2010, personal communication). GSM services are widely available in Europe and Asia. Unfortunately, there are many vast areas throughout the world (e.g. much of North America, Australia and sparsely populated Africa) without GSM services; thus, neither GSM/SMS nor GSM/GPRS are an option (http://www.gsmworld.com/technology/gsm/index.htm, accessed 25 February 2010; http://www.gsmworld.com/technology/roaming/gsminfo/index.htm, accessed 25 February 2010). Therefore, the most severe limitation is that animals might not encounter receiving towers (coverage zones), and therefore data collection can be intermittent or lost (Clark *et al.* 2006). Some systems now have 'failsafe modes' that allow older data to be data transferred when the animal returns to coverage. Note that secondary data network service GSM/GPRS is different from GMS/SMS and voice communications, and can have different coverage. GSM/GPRS data transfer systems continue to evolve, but typical data rates are in the range of 21.4–171 kbps (http://www2.rohde-schwarz.com/en/technologies/cellular_standards/GSM/information, accessed 25 February 2010).

Subscriber Identity Module (SIM) contains the subscriber's identity number, telephone number and the original network subscription. A SIM card can be exchanged with any handset (http://www.cisco.com/univercd/cc/td/doc/product/wireless/moblwrls/cmx/mmg_sg/cmxgsm.htm, accessed 25 February 2010). Most GSM systems typically use the 850–900 MHz or 1800–1900 MHz frequency range (http://www.gsmworld.com/technology/gsm/index.htm, accessed 25 February 2010). The system can also be used in a two-way manner, allowing the change of onboard collar parameters (Sundell *et al.* 2006).

(v) *Data recovery using LEO satellite telephone data services*

Because there are many regions of the world without GSM coverage, commercial businesses provide satellite-based telephone systems. Two such systems, Iridium and Globalstar, include data services that are potentially useful for data transfer from animal applications. Both services are on LEO satellite systems and offer advantages over Geosynchronous (GEO) systems for delivering mobile satellite services (MSS). These advantages result from orbits that enhance the quality of services to low-power mobile hand-held and vehicle-mounted equipment. GEO satellite systems, at altitudes of 35 800 km, are best suited for high-speed data, television transmission and other wideband applications. Unless the GEO satellite has high-gain directional antennas, it is unable to receive from small handsets with omnidirectional antennas.

Commercial off-the-shelf hand-held satellite telephones are not suitable for deployment on animals. Biotelemetry manufacturers must procure certified modules from large-scale manufacturers and access to the system must be contracted. It is often difficult to integrate data transfer in animal-borne applications, given the limitations in hardware and firmware designs that are optimized for non-animal applications, especially deploying and maintaining an antenna on an animal. The integration process is not trivial.

(vi) *Data transfer using Iridium satellites*

The Iridium constellation currently provides mobile two-way data links for tracking and monitoring. Iridium Satellite LLC is a privately owned company providing worldwide, two-way, near-continuous coverage for voice and data communications. A short burst data (SBD) service, analogous to text messaging, is also available (Meldrum *et al.* 2003). Iridium's current constellation is 66 LEO, cross-linked satellites, plus replacement spares. The satellites are in a near-polar orbit at an altitude of 780 km in six orbital planes, evenly spaced around the Earth. Each plane has 11 satellites equally spaced and a single satellite circles the Earth every 100 min, at 16 832 miles h^{-1}. A satellite is visible to a stationary ground terminal for about 10 min, and, as it goes over the horizon, a call is transferred to the next satellite. Each Iridium satellite is cross-linked to four others to create a dynamic network in space.

Iridium is used in oceanographic applications in dial-up and in short-burst mode. Iridium has small low-profile antennas associated with the 1.5 GHz frequency communications link and the two-way link either via a command in dial-up or simple handshaking mode in SBD. Current technology is suitable for larger terrestrial species such as caribou (Aastrup 2009). We found two manufacturers (www.vectronic-aerospace.com, accessed 31 January 2010; www.lotek.com, accessed 1 February 2010) offering data transfer and animal unit reprogramming capability via Iridium.

(vii) *Data transfer using globalstar satellites*

Globalstar is a phone system suitable for mobile applications, consisting of more than 40 LEO satellites. Handsets operate with hand-held, vehicle-mounted telephone devices using omnidirectional antennas. Calls and data links are passed from one satellite to another, enabling the Globalstar system to provide service to locations including some with signal blockage from buildings, terrain or other natural features. The greatest limitation is that there are areas in the world without coverage. From the satellite, data are transmitted to land-based receiving stations called Gateways, where further data management occurs and information is prepared for distribution to the user. The location of Gateways determines where the Globalstar system provides geographical coverage.

The Simplex data and asset tracking services section of the Globalstar system is used for wildlife telemetry. Globalstar Simplex sends data at a speed of 100 bps and allows limited messaging. Globalstar uses code division multiple access (CDMA) technology. User terminals share time and frequency allocations and access to the network. Signals are separated at the receiver by a correlator that accepts a signal from a single terminal, while excluding other signals. Wildlife telemetry manufacturers program the GPS-Globalstar units to transmit the same GPS-based location message to the satellites up to four times to increase the probability that the message has been received at the satellite.

GPS-Globalstar collars can transmit every GPS location acquired in real time from the field to the internet, or log and store location estimates for later retrieval. For example, a unit could be programmed to acquire a GPS location eight times per day and to transmit one GPS location per day or per week, thus conserving battery power and costing less for data delivery via the satellite system. The Globalstar Simplex services are designed to work with the second-generation satellite constellation to provide users with service into the next decade.

Wildlife collars using a GPS-receiving antenna and a Globalstar patch-transmitting antenna have recently become available and are being used on many projects, but we are unaware of the published results. We borrowed four wildlife collars that incorporated GPS receivers with transmitters that sent data through the Globalstar satellite system (North Star Science and Technology, http://www.northstarst.com/default.aspx, accessed 31 January 2010). We monitored these units on the flat roof and received data from 100 per cent of the transmissions to the Globalstar system. Two units provided 39 location estimates and two provided 40 estimates. The minimum location error for all four was 0.455 m and the average maximum error was 7.5 m (range 6–10 m). The 75th percentile error average was 4.8 m.

(viii) *Node-to-node networking*

Another approach to data transfer is found in mobile *ad hoc* networks (Pelusi *et al.* 2006). It is possible to configure each of the deployed devices (e.g. large mammal collar) as a separate node in a mobile network. The nodes then communicate with each other as links that are available on a specific schedule, resulting in each device having stored location data from all other devices current as of the last set of communications. When the behaviour of the animals brings the devices into proximity with each other, remote retrieval of data from all marked animals depends only on querying one device rather than all the network nodes. This approach has been used on a limited basis with zebras (*Equus quagga*; http://www.princeton.edu/~mrm/zebranet.html, accessed 31 January 2010; Juang *et al.* 2002; Martonosi 2006; Hari *et al.* 2008) and wood turtles (*Clemmys insculpta*; http://prisms.cs.umass.edu/dome/index.php?page=TurtleNet, accessed 31 January 2010).

5. THE BRAVE NEW WORLD OF WILDLIFE TELEMETRY

GPS positioning and data collection for animal research developed as commercial GPS and other diverse technologies matured. The success of animal-borne systems depended on experience with earlier tracking technologies (e.g. conventional VHF and Argos). Similarly, future advances will draw on the technology we have described here and on the new developments. Changes in GPS technology are ongoing and accompanied by changes in the GPS OEM manufacturing community. New global navigation satellite systems (GNSS) including Glonass, Galileo and Compass are emerging, with the potential to be used for animal positioning. Telemetry designers and manufacturers must select the appropriate technologies available from commercial and military sources, and integrate them into specialized instruments with rigorous performance requirements specific to an ever-increasing number of species, environments and biologists' objectives. Biologists must evaluate these offerings from a cost–benefit perspective. Widely varying study designs require specific attributes from sensors and the GPS and data transfer systems. Surveying the specifications allows the user to choose the most efficient system in terms of operational life, unit size and cost per data point.

Animal research continues to benefit from the large commercial market driving GPS development. There are significant advances in receiver technology roughly every six months with trends for GPS receivers getting smaller, operating at lower voltages, consuming less power and exhibiting reduced TTFFs. Advances like these will contribute to methods to study smaller terrestrial, marine and avian species (e.g. Vyssotski *et al.* 2006).

However, there are costs associated with producing products for animal studies. Each GPS manufacturer has proprietary hardware and software components. Evaluating the suitability is time-consuming and expensive for those integrating technology for animal applications. Most of the cost of developing new systems is for software development. In addition to this expense, constantly adapting products poses hidden unknown risks to the developer and the user.

The product lifetime of many electronic components has decreased from 10–15 years to about 12–18 months since 1980. To hedge against this rapid obsolescence at the component level, most manufacturers must buy a lifetime stock of some components to try to stabilize technology perhaps for a year or two. Change is inevitable; some industrial trends suggest that stand-alone GPS engines will cease to exist in the next 3–6 years. GPS technology is being assigned a peripheral role on highly integrated communications chips, as has happened to some degree in the mobile phone market.

Thus, electronic parts are continually becoming obsolete, causing telemetry manufacturers to replace parts that work well with new parts that have great features, but may not be fully tested in rigorous animal environments. Advanced parts might have additional features (lower current and voltage requirements, faster and smaller microprocessors, and lower quiescent current and lower dropout voltages) for, in theory, better unit performance. The potential downside is that highly customized radio telemetry systems, including software, require long-term testing in the variety of unique ranges of conditions that occur among free-ranging species. Best practice and thorough testing notwithstanding, natural environments expose the system to unforeseen problems. With so many new telemetry manufacturers appearing in the marketplace, engineers must be cognizant of the 'leap' that occurs when taking new equipment from the laboratory to the field. Manufacturers should introduce the technology as 'new', or in some cases 'experimental', and be certain that the studies making first deployments are aware of the risks involved in being on the 'cutting edge'. For studies that cannot take the risk, there is usually much greater reliability in products with a few years of field history. Wildlife radio telemetry stretches the performance of parts to and sometimes beyond the edge of their specifications, and is more likely to encounter aberrations than are the many commercial applications for which most components were designed. All of these factors combine to create a legitimate concern about fielding a new generation of products.

Welcome to a brave new world where change is rapid. Biologists who are procuring GPS technology must consider manufacturers based on previous performance, and hope that a manufacturer continues to conduct thorough laboratory testing and learns from field reports. Manufacturers should be notified promptly when problems arise in the field. Affected units are invaluable in the analysis, but most manufactures know it is not always possible to re-acquire units from the field. Good descriptive information of the observed symptoms and times when they occur can focus attention on the specific part of the system and can be invaluable in distinguishing between problems with sensors, battery or power supply, GPS receiver or antenna, and data transfer systems. Sometimes this information is adequate for the manufacturer to make a diagnosis even without the unit in hand. In any case, a working partnership between the telemetry manufacturer and the biologist can often lead to resolving the problem or minimizing the impact on the study. This cooperative approach can also result in the manufacturer fixing the previously unknown problem and avoid fielding the same problem in another study. Finally, when planning follow-on studies, biologists must be aware that equipment availability will change and that equipment capability and performance will also change when new components or new designs are implemented.

6. WHAT THE BIOLOGIST CAN DO IN THIS BRAVE NEW WORLD

We recommend that biologists correspond with wildlife telemetry equipment manufacturers to learn about current technology and discuss how it can help address study objectives. Useful guidance for selecting equipment can be obtained from the literature about radio-marking of the same species or similar species. Biologists must be aware that system design, including size and weight, can influence animal behaviour, reproduction and survival, and can affect results (Murray & Fuller 2000; Wilson & McMahon 2006; Brooks *et al.* 2008; Casper 2009). To minimize the effects of radio-marking on the animal, biologists can discuss with manufacturers details such as required operation life, form-factors, method of attachment, the mass of the animal and, thus, limitations on telemetry unit size and allowable transmitter antenna length. We suggest providing the manufacturer with information about the study environment, including study locations, operating temperature range and topography. Also, we advise inquiring about the manufacturing lead time to assemble and deliver the equipment. Employing new technology and innovations in animal research can be time-consuming, and the biologist will probably want to learn to use and to test performance of new methods and equipment before investing in capturing, marking and releasing free-ranging animals.

Telemetry system performance is important information for designing studies (Ryan *et al.* 2004; Mills *et al.* 2006; Horne *et al.* 2007; Mitchell & Powell 2008; Godvik *et al.* 2009). If the user is unfamiliar with the equipment, or if it is being used for the first time on a species or in an unusual landscape, ample time should be allowed to test functions of the radio telemetry 'system'. From the receiver–logger–transmitter unit to data delivery, there are many components and interactions, including environmental factors that influence how a system functions. Manufacturer testing and nominal specifications are often different from performance outside the laboratory or on the animal. We encourage biologists to report negative and positive results to the manufacturer, and ultimately to publish failure rate and performance results (e.g. Gau *et al.* 2004).

GPS capability, the large capacity of datalog memory and data transfer technology enables high sampling rates, such as one fix every 15 s. Managing high volumes of data is an important consideration in terms of cost and data security (Urbano *et al.* 2010). Automated data reception and handling methods are available from some services (e.g. Argos) and manufacturers, and some projects have created custom procedures. Testing systems before placing the units on animals, and pilot studies with animals in the field, can ensure that users are familiar with equipment operation and data acquisition, and that performance is acceptable for the users' objectives. For example, when solar charging is often used to prolong the operation life of the unit, which is common for bird studies (Cadahia *et al.* 2007), many factors can affect the regularity and extent of charging (e.g. hours of light, cloud cover).

There are limitations to GPS positioning, the most significant of which is the inability to obtain a position fix when obstructions occur between the signal from the satellites and the GPS receiver (e.g. under dense canopy, inside dens, topography; D'Eon *et al.* 2002; Hebblewhite *et al.* 2007; Frair *et al.* 2010). Fix rates and location errors vary depending on environmental circumstances. Equipment testing in the study environment can reveal factors that might influence performance in various situations and thus be informative for study design (Cain *et al.* 2005; Cargnelutti *et al.* 2007; Hebblewhite *et al.* 2007; Sager-Fradkin *et al.* 2007; Hansen & Riggs 2008).

Tests such as these provide indications of the variability in performance within and among units, and test data can be useful for interpreting results. However, we agree with Cargnelutti *et al.* (2007) that standardized tests almost certainly overestimate performance compared with performance of units on free-ranging animals, when additional variation can be expected. GPS has been integrated with VHF and video to assess how equipment performs on free-ranging animals (MacNulty *et al.* 2008). Furthermore, biologists should plan the number of animals to be marked based on an expectation of some loss of data caused by the death of animals and equipment failure.

Rapid advances in positioning, sensor and data transfer technologies are being applied to the study of animal behaviour and ecology. GPS can provide accurate, regular and frequent estimates of locations for movement ecology research into many species of animals. For the promise of new GPS, emerging GNSS and associated technologies to be fulfilled, engineers and biologists will need to work in partnership, share needs, understand limitations and be aware of emerging opportunities.

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GLOSSARY

Almanac: parameters contained in the navigation message that allow a GPS receiver to approximate the general positions of all the GPS satellites.

CDMA: code division multiple access is the standard mobile voice and data transfer technology used in the USA and parts of Asia.

Cold start: a condition where the GPS receiver attempts to begin the navigation process without the assistance of any almanac information, time, location or current ephemeris stored in its memory.

DCLS: the Argos data collection and location system.

DGPS: differential GPS is a technique to reduce the error associated with a GPS position determination by providing additional information obtained from a GPS receiver at a precisely known position.

Ephemeris: correction term applied to the modified elliptical orbit model to account for perturbations of the orbit of a satellite. The navigation message from each GPS satellite includes a predicted ephemeris for the orbit of that satellite valid for the current hour. The ephemeris is repeated every 30 s.

FM: frequency modulation is a radio frequency data modulation technique used to transfer data.

GPS: global positioning system is a positioning system operated by the USA.

GSM: a TDMA (time division multiple access) global system for mobile communication. The standard mobile telephone and data transfer system used in Europe, Asia and Africa.

Hot start: a condition where a GPS receiver begins navigation with current almanac, time, location and ephemeris.

LEO: low-earth-orbit refers to satellites in orbits close (160–2000 km) to the Earth. LEO satellites pass over regions of the Earth but are not in continuous view from a single point on the Earth's surface.

MDAC: micro-power data acquisition/controllers are specialized microprocessors that are embedded in small battery-powered mobile devices.

Navigation message: a message included in the GPS signal including the satellite ephemeris, clock data, almanac and some other data.

OEM: original equipment manufacturer refers to a company that acquires a product or component and reuses or incorporates it into a new product with its own brand name.

Pseudoranges: a measurement of the time difference between satellite clock time and the GPS receiver onboard the animal based on a microwave transmission.

QFP: quick fix pseudoranging is a rapid fix technique that is used to obtain pseudoranges from a GPS receiver. The pseudoranges and appropriate ephemeris data are used to calculate a GPS position at a later time.

SA: selective availability is a policy and procedure of denying non-military users full accuracy of the GPS system.

SOB: store onboard units obtain GPS-based locations and/or sensor data that are retained in the onboard memory for later download.

SST: spread spectrum technology is a wireless high-speed two-way data transfer technique with the advantage that it minimizes interference between multiple units deployed in the same area.

Triangulation: a positioning technique commonly used to establish position of animals instrumented with conventional very high frequency telemetry. The technique involves establishing the point of intersection of three or more bearings taken from different receiving locations.

TTFF: time to first fix is used as a measure of how long it takes a GPS receiver to obtain its position after being powered up.

VHF: very high frequency refers to a wildlife tracking technology that uses frequencies in the range of 30–300 MHz to locate and track animals.

Warm start: the condition wherein a GPS receiver begins navigating using the current almanac, time and position stored in its memory from previous use, but without the benefit of having current ephemeris.